Seed Type and Seed Surface Patterns in *Calandrinia* sens. lat. (Portulacaceae)

SYEDA SALEHA TAHIR and ROGER CAROLIN

SYEDA SALEHA TAHIR, & CAROLIN, ROGER, Seed type and seed surface patterns in *Calandrinia* sens. lat. (Portulacaceae). *Proc. Linn. Soc. N.S.W.* 110 (4), (1988) 1989: 307-316.

Seed types of *Calandrinia* are defined as six shapes which are determined by the shape of the embryo and the amount of perisperm present. Ten surface patterns are described and the presence or absence of an aril are considered. The species usually have characteristic shapes and surface patterns but these features rarely characterize the segregate genera or the sections. Within some of the segregate genera and sections, however, there appear to be definite, and sometimes characteristic, phylogenetic trends in these features.

Syeda Saleha Tahir and Roger Carolin, John Ray Herbarium, University of Sydney, Australia 2006; (Syeda Saleha Tahir, new address, *Botany Department, University of Sind, Jamshoro, Sind, Pakistan);* *manuscript received 14 September 1987, accepted for publication 23 March 1988.*

INTRODUCTION

Seed type and seed surface pattern have been used extensively in plant taxonomy. Carolin (1987) has shown that the former, in particular, is useful at the generic level in the family Portulacaceae and has indicated that in certain genera, surface pattern can be useful in distinguishing between species (see also Cullen, 1953). Furthermore, the aril or strophiole, in this case derived from the funicle, has been used in the past to discriminate between genera, e.g., Pax and Hoffman (1935). This investigation seeks to establish the use of these features for the taxonomy within the genus *Calandrinia.*

The genus *Calandrinia* consists of about 130 species of which about 50 occur in Australia. Carolin (1987) has suggested that the genus be divided into five genera, *Calandrinia* sens. strict., *Cistanthe*, *Baitaria*, *Schreiteria* and *Rumicastrum.* The necessary combinations have not been made, except in *Schreiteria*, and here they will all be referred to as *Calandrinia* with the segregate name in parentheses. Although seed surface pattern has been used in the past to distinguish between some Australian species, e.g., Black (1948) and Reiche (1888), the only general survey of either seed type or surface pattern in these species is that of Syeda (1980). This contribution details the variation in these characters, provides a terminology and suggests a phylogeny for these characters.

MATERIAL AND METHODS

The mature seeds were taken from herbarium specimens and mounted on a stub with double sided sticky tape. They were then coated with 200-400 Å thickness of gold in a polaron coating machine and examined with a JSM-U3 scanning electron microscope. Two to three samples from different collections were examined for 77 species in this manner but in most cases only one voucher is listed here (Table 1). Where available, the seeds of most specimens of each species were examined using a stereo-microscope to check for variation within a species.

Hand sections were cut to ascertain the shape of the embryo and the distribution of the perisperm.

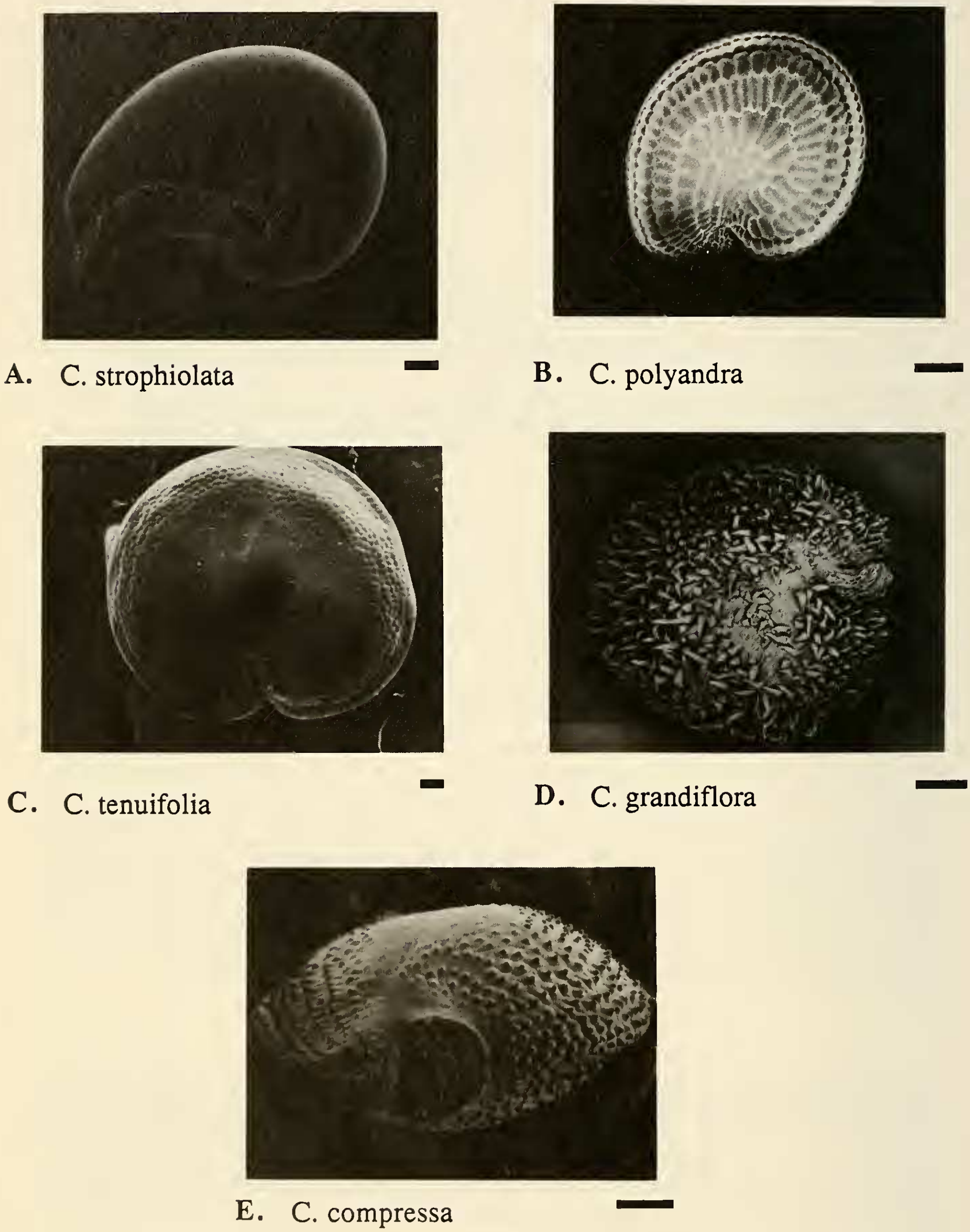

Fig. 1. **A.** *C. strophiolata*; **B.** *C. polyandra*; **C.** *C. tenuifolia*; **D.** *C. grandiflora*; **E.** *C. compressa*. (Bars indicate 100μ).

Results

SEED SHAPES

The seed shape presented some problem since the differences between species, though often clear, are relatively slight and difficult to describe in words. The shapes defined in the chart of plane shapes reproduced in Stearn (1966) are not entirely satisfactory for 3-dimensional objects. Nevertheless, many workers do use them in this context, usually apparently referring to the projected shadow across the long axis. The shapes of *Calandrinia* seeds, however, do not always correspond to the standards even when thus projected onto a plane. Stearn also provides a chart of spore shapes from Ainsworth and Bisby; where these terms apply we have used them. Moreover some of the shapes integrade with each other and the decision as to their classification in some cases is a little arbitrary. The terms are redefined below in this particular context and illustrated in Figs 1 and 2.

Seed shape is a function of the shape of the embryo and, to a lesser extent, the amount of perisperm. The curvature and length of the embryo, and the relative growth of the radicle in relation to the cotyledons, determine the position of the funicle. The schematic diagrams in Fig. 3 illustrate this:

Oblong/Orbicular: Embryo almost completely encircling the perisperm; funicle attachment symmetrical at the base; ± compressed. The two shapes intergrade closely, e.g. *C. oblonga* (Fig. 2**F**). See Fig. 3**A**, **B**.

Notched Oblong/Orbicular: As for oblong but growth of both radicle and cotyledons continued below the funicular attachment, giving a basal notch, e.g. *C. tenuifolia* (Fig. 1**C**), *C. polyandra* (Fig. 1**B**). See Fig. 3**C**.

Obovoid to globular: Embryo almost encircling the perisperm but growth of the radicle continued below the funicular attachment thus causing the latter to be asymmetric; sometimes this distortion becomes extreme; not or very little compressed, e.g. *C. ptychosperma* (Fig. 2**C**), *C. reticulata* (Fig. 2**D**), *C. grandiflora* (Fig. 1**D**). See Fig. 3**D**.

Asymmetric clavate: Embryo not quite encircling the perisperm, funicle attached to one side of a basal point; not compressed, e.g. *C. lehmannii.*, This represents a type intermediate between obovoid/globular and curved.

Curved: Embryo not encircling perisperm but curved distally; funicle attached to one side of a basal point; not compressed, e.g. *C. primuliflora* (Fig. 2**E**). See Fig. 3**F**.

Narrow-obovoid: A very narrow seed but similar to the obovoid form described above; scarcely compressed, e.g. *C. disperma*.

There are, of course, intermediate states, some of which may indicate phylogenetic series.

SEED SURFACE PATTERN

Here also the terms described by Stearn (1966) for surface patterns need some amendment as defined below:

Smooth: No prominent pattern, the outline of the epidermal cells usually visible but the surface between the radial walls flat, e.g. *C. strophiolata* (Fig. 1**A**).

Colliculate: The surface of each epidermal cell is slightly raised into a shallow dome forming a closely packed pattern, e.g. *C. polyandra* (Fig. 1**B**).

Reticulate: The radial walls of each epidermal cell are raised into a ridge, e.g. *C. reticulata* (Fig. 2**D**).

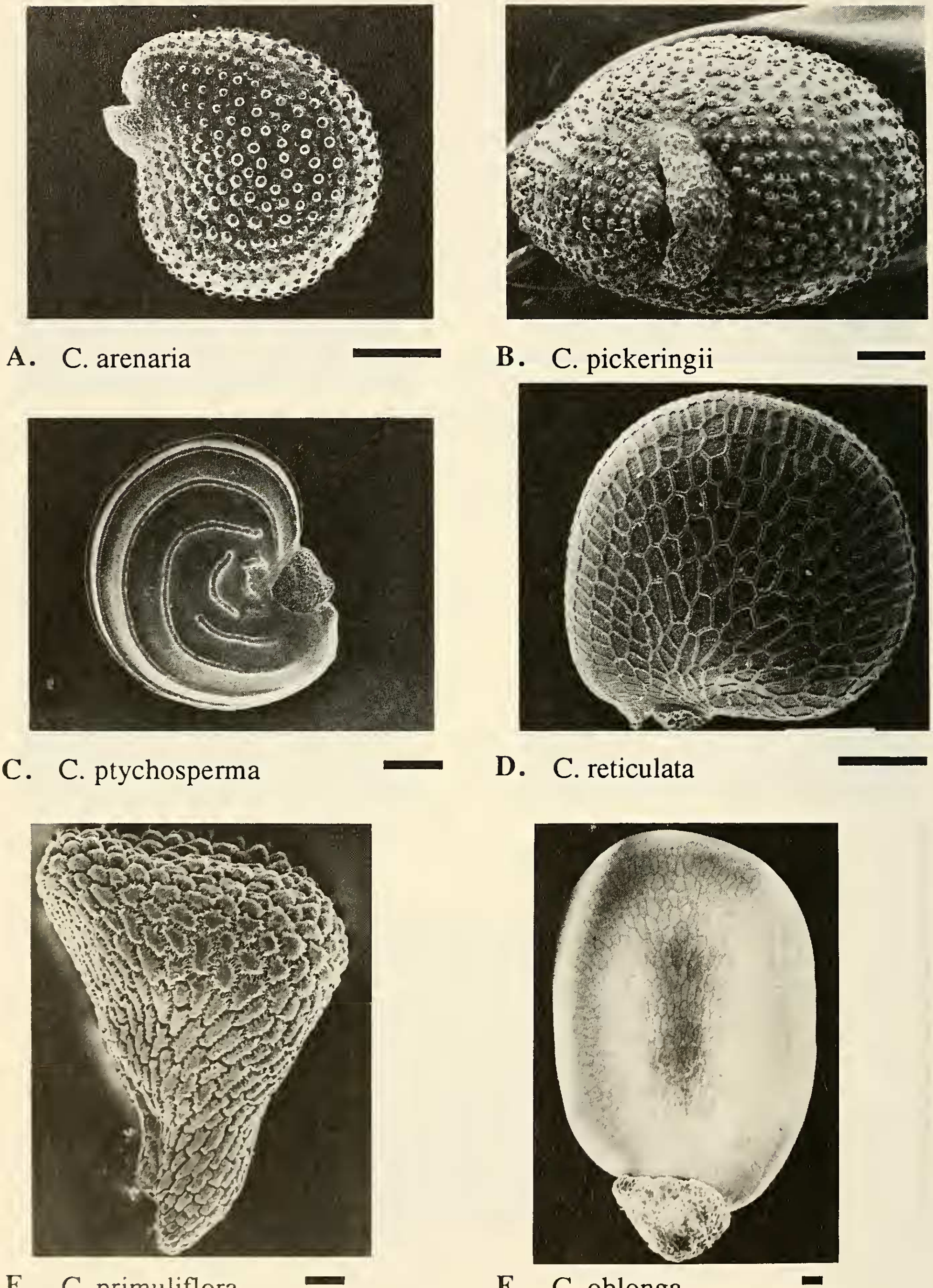

Fig. 2. **A.** *C. arenaria*; **B.** *C. pickeringii*; **C.** *C. ptychosperma*; **D.** *C. reticulata*; **E.** *C. primuliflora*; **F.** *C. oblonga*. (Bars indicate 100μ).

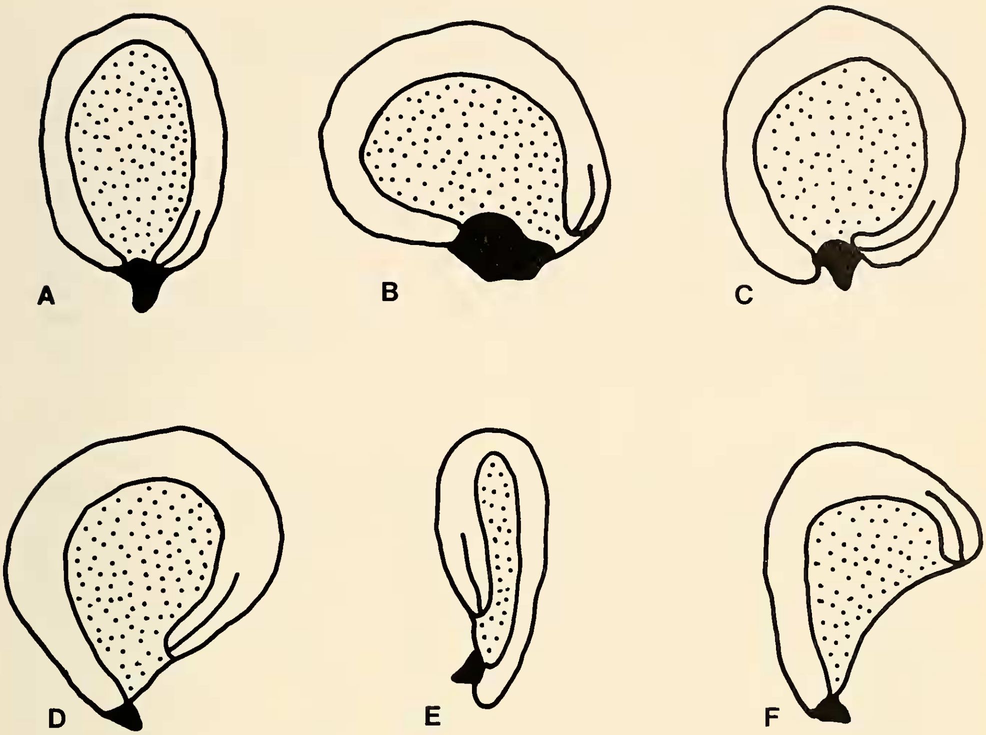

Fig. 3. Schematic diagrams to show seed shape and its associated features. **A.** Oblong/(orbicular); **B.** (Oblong)/orbicular: **C.** Notched oblong/orbicular; **D.** Obovoid; **E.** Narrow obovoid; **F.** Curved.

Papillate: The centre of the outer tangential wall of the epidermal cell is projected into a short rounded papilla e.g. *C. compressa* (Fig. 1**E**). Generally the cells of the epidermis tend to be aligned into rows and thus, so do the papillae. In some species this is more pronounced than in others and in this case the pattern may be referred to as aligned-papillate, e.g. *C. arenicola*.

Aculeate: Similar to tuberculate in which the papillae are extended into a long narrow hair-like process, e.g., *C. grandiflora* (Fig. 1**D**).

Polypiform: In this case the papillae have short lobes over their surface, e.g., *C. arenaria* (Fig. 2**A**).

Papillate-punctate: Similar to papillate but with a small pit at the corner junctions of each cell, e.g. *C. pickeringii* (Fig. 2**B**).

Ribbed: The surface is marked by prominent ribs which are the confluent papillae of adjacent aligned cells, e.g. *C. ptychosperma* (Fig. 2**C**).

Tuberculate: The papillae project into broad finger-like processes e.g. *C. lehmannii*.

Verrucate: Similar to tuberculate but the tubercles are somewhat shorter and, although the top is smooth, the sides are ridged as though they were thinner, thus giving a warty appearance, e.g. *C. primuliflora* (Fig. 2**E**).

ARIL

It is often difficult to determine whether an aril is present or not since small fragments of the funicle may be left on the seed due to the abscission occurring well below the insertion of the funicle on the seed. The fragment left may or may not function as an elaiosome in ant dispersal. It seems possible that a well developed aril is an elaiosome as in *C. grandiflora* (Carolin, pers. obs.). This true aril is the swollen upper part of the funicle and the primary abscission occurs below it; this is registered as '+' e.g. *C., ptychosperma* (Fig. **2C**), *C. strophiolata* (Fig. **1A**), *C. grandiflora* (Fig. **1D**), *C. arenaria* (Fig. **2A**). When only a slight swelling, or none at all, occurs above the primary abscission but a fragment of funicle remains on the seed this is registered as '±' e.g. *C. polyandra* (Fig. **1B**). When the primary abscission occurs at the insertion of the funicle on the seed this is registered as '–' e.g. *C. tenuifolia* (Fig. **1C**), *C. compressa* (Fig. **1E**), *C. primuliflora* (Fig. **2E**).

The results are summarized in Table 1, in which the Australian species are grouped according to the sections of Syeda (1980) and the others are grouped according to Carolin (1988).

TABLE 1

Species examined for seed characteristics in the course of this investigation

(Vouchers are given using the herbarium number where one is available. Where one is not available the herbarium is indicated and the collector and collector's number are given. Herbarium codes are taken from Index Herbariorum)

Species name	shape	pattern	aril	Voucher
Calandrinia (*Cistanthe*) sect. Cistanthe				
C. arenaria Cham.	obov	Sm/Co	+	CONC 47320
C. cachinalensis Phil.	obov	Po	+	NO VOUCHER
C. coquimbensis Barn.	obov	Ac	+	NO VOUCHER
C. frigida Barn.	obov	Pp	+	CONC 32814
C. glaucopurpurea Reiche	obov	Po	+	NO VOUCHER
C. grandiflora Lindl.	obov	Ac	+	Carolin 14022 SYD
C. litoralis Phil.	obov	Po	+	CONC 47322
C. longiscapa Barn.	obov	Po	+	NO VOUCHER
C. maritima Nutt.	obov	Ac	+	NO VOUCHER
C. oblongifolia Barn.	obov	Po	+	Carolin 14112 SYD
C. solisii Phil.	obov	Po	+	NO VOUCHER
C. thyrsoidea Reiche	obov	Ac	+	CONC 8396
Calandrinia (*Cistanthe*) sect. Amarantoideae				
C. ambigua Nutt.	obov	Pp	–	B 1417582
C. calycina Phil.	ob/or	Sm/Co	–	CONC 33144
C. spicigera Phil.	ob/or	Sm/Co	–	CONC 47320
Silvaea pachyphylla Phil.	ob/or	Sm/Co	–	CONC 9365
Calandrinia (*Baitaria*) sect. Dianthoideae				
C. andicola Gill. ex Arn.	n.ob/or	Sm	–	CONC 49244
C. cistiflora Gill.ex.Arn.	n.ob/or	Co	–	CONC 3200
C. gayana Barn.	n.ob/or	Co/Sm	–	CONC 4898
C. patagonica Speg.	ob/or	Co	–	CONC 34827
C. tenuifolia Phil.	n.ob/or	Co	–	CONC 32104
Calandrinia sens. strict.				
C. axilliflora Barn.	obov	Pp	±	CONC 49732
C. compressa Schrad.	obov	Pp/Co	±	Carolin 14000 SYD
C. ciliata (Ruiz & Pavon) DC.	obov	Co	±	Carolin 14090 SYD
Calandrinia (*Baitaria*) sect. Hirsutae Hook. & Arn.				
C. sericea Hook. & Arn.	obov	Co	–	Carolin 14121 SYD
C. umbellata (Ruiz & Pavon) DC.	obov	Sm	–	Boelcke 13859 SYD
C. uspalatensis Phil.	obov	Co	–	Carolin 14090 SYD

TABLE 1 (continued)

Species name	shape	pattern	aril	Voucher
Calandrinia (*Baitaria*) sect. Condensatae				
C. capitata Hook. & Arn.	ob/or	Sm	–	Carolin 14011 SYD
C. demissa Phil.	obov	Pp	–	CONC 8568
C. floribunda Phil.	obov	Co	–	Carolin 14109 SYD
C. glomerata Phil.	ob/or	Co	–	CONC 41891
C. leucocephala Phil.	ob/or	Co	–	Carolin 14108 SYD
C. modesta Phil.	obov	Co	–	CONC 32801
C. polycarpoides Phil.	obov	Co	–	CONC 32732
C. prostrata Phil.	obov	Co	–	CONC 32747
C. trifida Hook. & Arn.	ob/or	Co/Sm	–	Carolin 14024 SYD
Calandrinia (*Baitaria*) sect. Acaules				
C. acaulis (Ruiz & Pavon) HBK.	obov	Pp	±	LIL 408812
C. affinis Gill. ex Arn.	obov	Sm/Co	±	Carolin 14013 SYD
C. affinis Gill. ex. Arn.	obov	Pp	±	Carolin 14014 SYD
C. caespitosa Gill. ex Arn.	obov	Co/Sm	–	Carolin 14122 SYD
C. fuegiana Gand.	obov	Co	–	CONC 32743
C. megarrhiza Helmsl.	obov	Co	–	RSA 631344
Calandrinia (*Rumicastrum*) sect. Pseudodianthoideae				
C. arenicola Syeda	n.ob/or	Ap	+	TYPE BRI 108559
C. balonensis Lindl.	n.ob/or	Co	±	AD 96923308
C. brevipedata F. Muell.	ob/or	Sm	±	TYPE MEL 48539
C. calyptrata Hook. f.	ob/or	Sm	±	AD 97314277
C. composita (Nees) Benth.	n.ob/or	Co	±	TYPE MEL 48615
C. corrigioloides F. Muell. ex Benth.	ob/or	Sm	±	TYPE MEL 48628
C. creethiae Morrison	obov	Sm-Co	±	C. A. Gardner 7821 PERTH
C. disperma J. M. Black	nr. obov (see text)	Co-Pp	–	P. G. Wilson 8414 PERTH
C. eremaea Ewart	n.ob/or	Pp	±	AD 96913076
C. granulifera Benth.	obov	Co	±	AD 96929529
C. liniflora Fenzl	ob/or	Sm	±	H. Demarz 2725 PERTH
C. monosperma Syeda	obov	Sm	–	TYPE PERTH
C. pickeringii Gray	obov	Pp-p	±	BRI 015191
C. pleiopetala F. Muell.	obov	Co	±	TYPE MEL 48743
C. polyandra Benth.	n.ob/or	Co	±	AD 96343036
C. pumila F. Muell.	obov	Sm-Co	+	TYPE MEL 48789
C. quadrivalvis F. Muell.	obov	Co	±	TYPE MEL 48799
C. remota J. M. Black	ob/or	Sm	P	AD 96416002
C. reticulata Syeda	obov	Rt	P	TYPE NT 43058
C. sphaerophylla J. M. Black	n.ob/or	Co	±	TYPE AD 97826032
C. stagnensis J. M. Black	obov	Sm-Co	±	TYPE AD 96846192
C. strophiolata F. Muell.	obov	Sm	+	TYPE MEL 48826
C. volubilis Benth.	n.ob/or	Pp	±	TYPE MEL 48860
Calandrinia (*Rumicastrum*) sect. Tuberosae				
C. lehmannii Endl.	as-c	Tb	–	T. L. Setter 427 PERTH
C. primuliflora Diels	cu	V	–	MEL 48774
C. schistorrhiza Morrison	cu	Tb	–	T. E. H. Aplin 2434 PERTH
Calandrinia (*Rumicastrum*) sect. Basales				
C. gracilis Benth.	obov	Co	±	BRI 053297
C. papillata Syeda	n.ob/or	Pp	±	TYPE PERTH
C. pleiopetala F. Muell.	obov	Co	±	TYPE MEL 48743
C. porifera Syeda	obov	Co	±	TYPE PERTH

TABLE 1 (concluded)

Species name	shape	pattern	aril	Voucher
C. ptychosperma F. Muell.	obov	Rb	+	W. E. Mulham W941 NSW
C. spergularina F. Muell.	obov	Co	±	TYPE MEL 48819
C. uniflora F. Muell.	ob/or	Sm	—	AD 96919061
Schreiteria				
S. macrocarpa (Speg.) Carolin	oblong	Co/pap	—	LIL Schreiter 4857

Abbreviations used for seed shapes:
as-cl = asymmetric-clavate; cu = curved; n.ob/or = oblong to orbicular with a notch at insertion of funicle; ob/or = oblong to orbicular, ± symmetric at base; obov = obovoid, ± asymmetric at base; nr. obov = narrow obovoid.

Abbreviations used for surface patterns:
Ac = aculeate; Ap = aligned papillate; Co = colliculate; Po = polypiform; Pp = papillate; Pp-p = papillate-punctate; Rb = ribbed; Rt = reticulate; Sm = smooth; Tb = tuberculate; V = verrucate. *Schreiteria* is coded differently to indicate that the surface and shapes here are not comparable with the others in the table.

DISCUSSION

This survey indicates that there is range of seed types and seed surface patterns in *Calandrinia* sens. lat., and that they have a significant role to play in species recognition.

Whilst the transformation series of seed shape and surface pattern are fairly clear, the polarization of these states, in the latter case at least, is not clear. The cladogram presented by Carolin (1987) indicates that the outgroup of the clade containing all of the segregate genera except *Schreiteria* is the *Portulaca* group of genera. This outgroup is equivocal for these characters. The outgroup of the whole family is Aizoaceae and little is published about the seed shape and surface patterns of this group.

Shape

There seems little doubt that curved shapes and those containing reduced endosperm are advanced features since they do not seem to occur in the Aizoaceae. The curved shape, together with the curved embryo and reduced perisperm, also occurs in the *Portulaca* group of genera (Carolin, 1987). The occurrence in the *Portulaca* group is considered to be a separate origin of the feature.

We suggest that the oblong/orbicular and notched-oblong/orbicular shapes may represent the primitive condition whilst obovoid represents an asymmetry of the embryo at the base of the seed; the asymmetric-clavate and curved shapes represent an increasing asymmetry of the embryo. The narrow-obovoid shape is a special case found together with a narrow clavate shape in the heterospermic species, *C. disperma*, whilst *Schreiteria macrocarpa*, has an oblong seed with a reduced perisperm thus making the seed much narrower than the other oblong types. These are derivative forms of the obovoid or oblong shapes and are not equivalent to the curved type with reduced perisperm, since the embryo still almost encircles the perisperm.

Seed surface pattern

The cladogram presented by Carolin (1987) is equivocal with regard to the primitive state of seed surface pattern. Both papillate and smooth patterns occur in *Calandrinia* (*Baitaria*) and evidence is lacking for Aizoaceae. Although it might seem more likely that the smooth condition is more primitive from a morphogenetic point of view, the evidence is slim. For the purposes of this description the smooth pattern is taken as a starting point but some amendment of this will probably be necessary as more characters of this group are considered.

The colliculate pattern is a derivation of smooth by the development of the surface into a dome. Papillate represents an upgrowth from this dome with aculeate, tuberculate and polypiform as further developments of that upgrowth. The papillate-punctate is a development from the papillate type as indicated above. The ribbed pattern is a development from the aligned papillate pattern as indicated above. The reticulate pattern is a quite separate development from colliculate/smooth patterns. Fig. 4 illustrates the putative evolutionary sequence in this character.

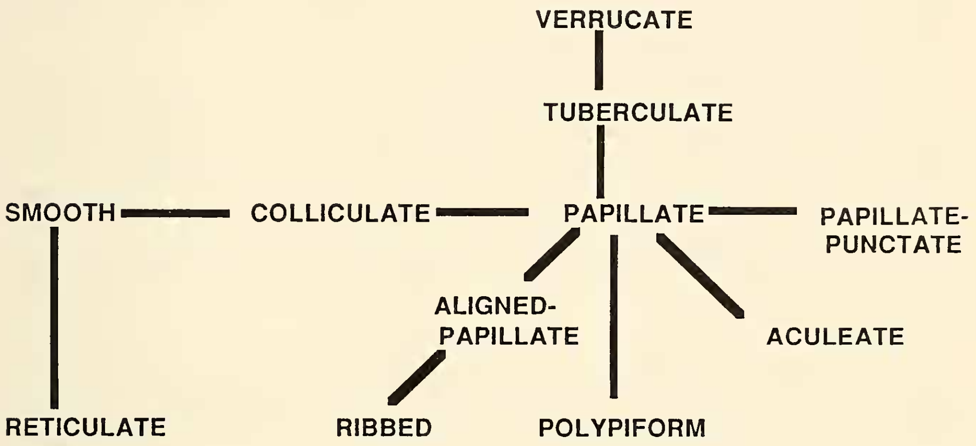

Fig. 4. The suggested transformation series of seed surface pattern.

Aril

It is equally difficult to conclude whether the presence or absence of an aril is primitive since the outgroups of both the family (see Corner, 1976) and the clade containing *Calandrinia* sens. lat. (Carolin, 1987), have arillate as well as exarillate seeds. It is probable that the aril is a response to particular dispersal requirements and if this is so the lack of it is likely to be primitive.

The segregate genera of *Calandrinia* sens. lat. are consistent neither in seed shape nor surface pattern and neither of these attributes thoroughly characterizes them. *Schreiteria* is monotypic with a more or less unique seed type having a very curved embryo with very little perisperm and a mostly colliculate surface with a few blunt papillae.

Calandrinia (*Baitaria*) consists mostly of species with colliculate or smooth surface patterns. Indeed, all those examined in sects Dianthoideae and Hirsutae have one of these two closely related patterns. One species in sect. Condensatae and two in sect. Acaules have papillate seeds. In fact, *C. affinis* at Farellones east of Santiago in Chile shows both papillate and colliculate surfaces in the same population.

Calandrinia (*Cistanthe*) shows several surface types. Within sect. Cistanthe there is a definite trend from smooth/colliculate through papillate to aculeate and polypiform surface. Most of the species have one or other of the two most advanced states. This trend is not shown in any of the other segregate genera. Even sect. Amaranthoideae has only smooth-colliculate and papillate surfaces. *Calandrinia* sens. strict. shows both papillate and colliculate surfaces.

Within *Calandrinia* (*Rumicastrum*) it is doubtful if the sections of von Poellnitz (1934) are natural. Syeda (1980) has suggested that there are only three recognizable sections within *Calandrinia* in Australia but this also may be open to question. The only section which is more or less consistent is sect. Tuberosae with a straighter embryo, less perisperm and a tuberculate or verrucate surface. Otherwise there would seem to be considerable homoplasy in these transformation series.

The aril may be of more use at the sectional level. All the species of *Calandrinia* (*Cistanthe*) sect. Cistanthe examined so far have arils. Likewise *Calandrinia* (*Cistanthe*) sect. Amaranthoideae, *Calandrinia* (*Baitaria*) sects. Dianthoideae, Hirsutae and Condensatae and *Schreiteria* do not have arils. The other taxa either have both conditions and/or have the indeterminate condition. It is clear, however, that one of the key characters provided by Pax and Hoffman (1935) to separate *Talinum* and *Calandrinia* (sens. lat.), viz., the presence or absence of an aril, is not satisfactory.

It seems, then, that the seed features are of limited value in distinguishing the segregate genera, although some genera and sections show distinct trends which, in the cases of *Calandrinia* (*Cistanthe*) and *Calandrinia* (*Rumicastrum*) sect. Tuberosae, are not repeated in other taxa at the same level. *C. pickeringii* and *C. reticulata* have unique surface patterns. The shape of the seed is also inconsistent within the segregate genera and sections except for *Calandrinia* (*Rumicastrum*) sect. Tuberosae, *Calandrinia* (*Cistanthe*) sect. Cistanthe and *Calandrinia* (*Baitaria*) sect. Acaules. *Schreiteria* occupies an isolated position within *Calandrinia* sens. lat. Indeed Carolin (1987) has suggested it is more closely related to the *Talinum* group of genera although the seed characters neither confirm nor contradict this.

It is clear from these results that the most variable of the segregate genera, with regard to seed shape and surface pattern, is *Calandrinia* (*Rumicastrum*). This greater variability is also shown in other characters such as fruit type and form of inflorescence.

ACKNOWLEDGEMENTS

We thank the Directors of the various Herbaria in Australia, Chile, Argentina, and U.S.A. who have lent material to us for this study from which seed samples have been taken. We thank also members of Universidad de Chile; Universidad de Concepcion; CEFAPRIN, Buenos Aires; Instituto Darwinion; Universidad de Cordoba and Instituto Lilloa for their help whilst RCC was engaged in collecting material for this study. In addition, we thank the staff of the Electron Microscope Unit at Sydney University for the use of their facilities, Tahir Rajput, Surrey Jacobs and Judy West for discussions on the work and Belinda Pellow and Cathy Miller for technical assistance. The University of Sydney provided funds which assisted in the investigation.

References

BLACK, J. M., 1948., — *Flora of South Australia*, ed. 2., vol. 2. Adelaide: Government Printer.

CAROLIN, R. C., 1987. — A review of the family Portulacaceae. *Austr. J. Bot.* 38: 383-412.

——, 1988. — Portulacaceae. *In* K. KUBITZKI, (ed.), *Families and Genera of Flowering Plants*. In press.

CORNER, E. J. H., 1976. — *The Seeds of Dicotyledons*, 2 vols. Cambridge: Cambridge University Press.

CULLEN, D. C. ANON SUAREZ DE, 1953. — Las especies argentinas del genero *Calandrinia* (Portulacaceae). *Bol. Soc. Arg. Bot.* 5: 1-112.

PAX, F., and HOFFMAN, K., 1935. — Portulacaceae. *In* A. ENGLER and H. HARMS, (eds), *Die naturlichen pflanzenfamilien*, ed. 2, 16c: 233-262. Leipzig: Engelmann.

POELLNITZ, K. VON., 1934. — Die Calandrinien-Arten Australiens. *Fedde Rep.* 35: 161-173.

REICHE, K., 1888. — *Flora de Chile*, vol. II. Santiago: Universidad de Chile.

STEARN, W. T., 1966 — *Botanical Latin*. London: Nelson & Sons.

SYEDA, S. T., 1980 — The genus *Calandrinia* HBK. in Australia. Sydney: University of Sydney, M.Sc. thesis, unpubl.